UNIVERSITY OF TECHNOLOGY SYDNEY

THE ECO-PHYSIOLOGY OF TWO CONTRASTING ARID-ZONE WOODLANDS IN AUSTRALIA

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Certificate of Original Authorship

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In memory of

Baltazar Terrazas Valdes (1956-2015), who had an incredible appreciation and passion for the natural world, and words cannot express how special he was for me.

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Abbreviations, acronyms and symbols

A	Carbon assimilation	(μmol m^{-2} s^{-1})
AIC	Akaike information criterion	
A_{max}	Maximum gross photosynthetic rates	(μmol m^{-2} s^{-1})
A_n	Net photosynthetic carbon uptake	(μmol m^{-2} s^{-1})
A_{n2000}	Net photosynthetic carbon uptake at PPFD= 2000 μmol photons m^{-2} s^{-1}	(μmol m^{-2} s^{-1})
ANN	Artificial neural network	
ANOVA	Analysis of variance	
BoM	Bureau of Meteorology	
C	Carbon	
C_a	Atmospheric CO_2 concentration	(μmol mol^{-1})
CFI	Comparative fit index	
C_i	CO_2 concentration inside leaf air spaces	(μmol mol^{-1})
CUE	Carbon-use-efficiency	(daily C gain *per* mol C fixed)
C3	Carbon fixation pathway where CO_2 is fixed by Rubisco	
C4	Carbon fixation pathway where CO_2 is fixed by PEP-Carboxylase	
CO_2	Carbon dioxide	
E	transpiration	(mol m^{-2} s^{-1})
EC	Eddy covariance	
ENSO	El Niño-Southern Oscillation	
ER	Ecosystem respiration	(gC m^{-2} d^{-1})
ET	Evapotranspiration	(mm)
ET_0	Reference ET	(mm)
EVI	Enhanced vegetation index	
D	Vapour pressure deficit at the leaf surface	(kPa)
D2, D3	Second and third drought, respectively	
DCG	Daily carbon gain	(mol C m^{-2} d^{-1})
G	Ground heat flux	(W m^{-2})
G_c	Canopy conductance	(mmol m^{-2} s^{-1})
GLSA	Global land sink anomaly	
GPP	Gross primary production	(gC m^{-2} d^{-1} or μmol mol^{-1})
g_0	Conductance when photosynthesis is zero	(mol m^{-2} s^{-1})
g_1	Optimal stomatal model inversely related to WUE_i	($kPa^{0.5}$)
g_s	Stomatal conductance	(mol m^{-2} s^{-1})
g_c	Stomatal conductance for CO_2	(mol m^{-2} s^{-1})
H	Sensible heat flux	(W m^{-2})
H_2O	Water vapour	
IRGA	Infrared gas analyzer	
LAI	Leaf area index	
LCP	Light compensation point	(μmol photon m^{-2} s^{-1})
LE	Latent heat flux	(W m^{-2})
LMA	Leaf mass *per* area	(g m^{-2})
LRC	Light response curve	
LSP	Light saturation point	(μmol photon m^{-2} s^{-1})
LUE	Light-use-efficiency	(mmol CO_2 μmol^{-1} photon)
MAP	Mean annual precipitation	
MODIS	Moderate resolution imaging spectroradiometer	
N, N_2	Nitrogen	
N_a	Foliar N concentration *per* leaf area	(g N cm^{-2})
NEE	Net ecosystem exchange	(gC m^{-2} d^{-1})

NEP	Net ecosystem production	(gC m^{-2} d^{-1})
P	Precipitation	(mm)
PAR	Photosynthetically active radiation	(µmol mol^{-1})
PDB	Pee Dee Belemnite	
PET	Monthly Penman-Monteith reference ET	
PFT	Plant functional type	
P_{gross}	Gross photosynthesis	(mol C m^{-2} d^{-1})
P_{net}	Net photosynthesis during the day	(mol C m^{-2} d^{-1})
PM	Penman-Monteith	
PNUE	Photosynthetic nitrogen-use-efficiency	((µmol CO_2) *per* (g N)$^{-1}$ s^{-1})
PPFD	Photosynthetic photon flux density	(µmol mol^{-1})
PPT	Rainfall	(mm)
QA/QC	Quality assurance/control	
R	Project software® for language statistical computing and graphics	
r_a	Aerodynamic resistance	(s m^{-1})
R_d	Dark respiration also R_{dark}	(µmol m^{-2} s^{-1})
R_{het}	Heterotrophic respiration	
r_L	Leaf resistance	(s m^{-1})
R_n	Net radiation	(W m^{-2})
R_{night}	Nocturnal respiration	
R_{plant}	Plant respiration	(µmol m^{-2} s^{-1})
R_{sample}	Ratio of heavy to light isotopes in a sample	
$R_{standard}$	Ratio of heavy to light isotopes in a standard	
RUE	Resource-use-efficiency	
SE	Standard error	
SEM	Structural equation modelling	
SPEI	Standardized precipitation-evapotranspiration drought index	
SOFM	Self-organizing feature map	
SOLO	Self-Organizing Linear Output	
SOM	Soil organic matter	(%)
SR	Solar radiation	(W m^{-2})
SWC	Soil water content	(m^3 m^{-3})
T_{air}	Air temperature	(°C)
TERN	Terrestrial Ecosystem Research Network	
TDR	Time-domain reflectometry	
u*	Friction velocity	(m s^{-1})
VPD	Vapour pressure deficit	(kPa)
VWC	Volumetric water content	(mm)
w	Vertical wind velocity	
WUE_i	Intrinsic water-use-efficiency	(µmol mol^{-1})
eWUE	Ecosystem water-use-efficiency	(µmol mol^{-1})
$_{int}$WUE	Instantaneous water-use-efficiency	(µmol mol^{-1})
WW	Well-watered treatment	
WS	Water-stressed treatment	
^{13}C	Carbon isotope with an atomic weight of 13	
^{12}C	Carbon isotope with an atomic weight of 12	
a	Fractionation during CO_2 diffusion through the stomata	(‰)
b	Fractionation associated with reactions by Rubisco	(‰)
β	A function for a scalar reduction of a process	(normalized from 0 to 1)
c_p	Heat capacity of moist air	
q	A parameter to describe the non-linearity of β	
q'	Mix concentration of CO_2 or H_2O	(g m^{-3})
γ	Psychrometric coefficient	

Ψ_{md}	Midday foliar water potential	(MPa)
Ψ_{leaf}	Diurnal foliar water potential	(MPa)
Ψ_{pd}	Pre-dawn foliar water potential	(MPa)
λ	Marginal water cost of plant carbon gain	(mol H_2O mol^{-1} C)
Γ^*	CO_2 compensation point	
ϕ	Quantum yield	(µmol CO_2 µmol $photons^{-1}$)
Δ	Stable isotope discrimination or $\Delta^{13}C$	(‰)
δ	Delta-isotopic notation	(‰)
σ	Standard deviation	
$\delta^{13}C$	Ratio of ^{13}C to ^{12}C	(‰)
$\delta^{13}C_{air}$	Carbon isotope ratio of the air	(‰)
$\delta^{13}C_{bulk\text{-}leaf}$	Isotopic compositions of bulk-leaf tissue	(‰)
$\delta^{13}C_{sugars}$	Isotopic compositions of leaf soluble sugars	(‰)
Q_A	Difference between net radiation flux and ground heat flux	
ρ_a	Density of moist air	(g m^{-3})
χ^2	Chi-square test for goodness of fit	

Abstract

Semi-arid and arid ecosystems occupy 45 % of the Earth's land surface and approximately 40 % of the global population live in arid and semi-arid regions. Ecosystem productivity in these regions is constrained by water availability, which is in general erratic, spatially variable and confined to short periods during the wet season. Globally, semi-arid and arid ecosystems dominate the inter-annual variability of the global land carbon (C) sink. In particular, Australian semi-arid and arid regions were estimated to account for 60 % of the 2011 global land carbon sink anomaly (GLSA). Despite the importance of these Australian arid and semi-arid environments, mechanisms that explain variability in rates of C uptake (at regional- and global-scales) and trends are poorly understood, and these ecosystems remain little studied.

Australia is an extensive and flat continent, of which 70 % is arid or semi-arid land. Two biomes dominate the central semi-arid region: (1) Mulga woodland, dominated by species of the genus *Acacia* (shallow rooted N_2-fixing trees, from the Mulga complex of species)*;* and (2) open *Corymbia* savanna where the dominant cover is spinifex (a C4 grass) with widely spaced tall evergreen *Corymbia* trees. These two ecosystems are found within the Ti-Tree Basin, Northern Territory Australia, where two eddy covariance systems has been in operation for the past 4 and 7 years within a Mulga woodland and *Corymbia* savanna respectively. The main objective of this research was to investigate ecosystem functioning of the two semi-arid woodlands, in order to improve our understanding of the interaction of terrestrial semi-arid ecosystems with the atmosphere, through measurements of C and water fluxes at ecosystem- and leaf-scales. The overall hypothesis was that differences in ecosystem vegetation composition and structure would be significant factors explaining differences in C and water fluxes across two disparate ecosystems. To accomplish this general objective, C and water fluxes were evaluated at different temporal-scales (i.e., diurnal, seasonal, annual and inter-annual) and different spatial-scales (from plot- to leaf-scales) within a Mulga woodland and a *Corymbia* savanna. I employed three different approaches to evaluate C and water fluxes: i) eddy covariance data (at plot-scale); ii) a range of *in situ* eco-physiological investigations (at leaf-scale); and iii) glasshouse experimentation (at leaf- and whole-plant-scale).

In 2011 during the GLSA, the Mulga woodland captured 131 g C m^{-2} y^{-1} and total annual precipitation was 565 mm. The most recent hydrological year studied (August to July 2016-2017) had the largest annual rainfall recorded during my monitoring of ecosystem fluxes (713 mm) and net ecosystem production (NEP) was 217 gC m^{-2} y^{-1}. In contrast to the Mulga woodland, the open *Corymbia*-savanna was a C source across most years (2012 to 2016), with

NEP ranging between -14 and -190 gC m^{-2} y^{-1}, but was a C sink during 2016-2017 with NEP of 115 gC m^{-2} y^{-1}. As a result of continuous monitoring of C fluxes, precipitation thresholds at which the two semi-arid woodlands switched from C source to C sink were identified for the first time. The pivot-point for the Mulga woodland was 262 mm y^{-1} and 506 mm y^{-1} for the *Corymbia* savanna.

The two semi-arid woodlands experience the same climatic conditions; hence, I observed that different climatic drivers (i.e., temperature, vapour pressure, soil water content) exerted similar influences over C and water fluxes across seasons. Intra-annual variability in C and water fluxes was mostly attributed to differences in SWC across seasons. However, different eco-physiological behaviours of co-occurring species within the Mulga woodland and *Corymbia* savanna contributed to explain differences in C and water fluxes between them. Dominant species at the Mulga woodland are highly adapted to periods of low water availability. Thus Mulga species were very water-use-efficient (WUE: trade-off between C gain *per* water loss) compared to species at the *Corymbia* savanna. This was demonstrated when evaluating responses of the g_1 parameter (as a proxy of intrinsic water-use-efficiency; WUE_i) to water availability. The Mulga woodland (at ecosystem- and leaf-scale) demonstrated large capacity for water consumption in wet periods and the plasticity to become highly WUE when experiencing water scarcity. In contrast, dominant species at the *Corymbia* savanna had larger water use (i.e., large stomatal conductance, at ecosystem-scale large rates of evapotranspiration) thus, smaller WUE compared to species at the Mulga woodland. The C4 spinifex grass can be highly productive at the *Corymbia* savanna during wet periods and, it is likely that the biomass produced during 2010-2011 was the fuel for photo-degradation of leaf litter, particularly of spinifex leaves in subsequent years, and this can explain the large negative NEP observed at the *Corymbia* savanna for much of the study period.

One of the novel aspects of the present research was to evaluate how soil water content drives WUE using the theory of the optimal stomata behaviour through the g_1 parameter (a normalized metric of intrinsic water-use efficiency: $_iWUE$) and compered g_1 values estimated from three different methods (leaf gas exchange, carbon isotopes and eddy covariance fluxes). Here my result showed discrepancies among methods and seasons. Thus, Seasonal and annual variation in *g1* derived from the three methods in this present study highlights the concern that the generic use of constant values of g_1 to describe stomatal functioning is not reliable when parameterizing global climate models (Medlyn *et al.*, 2017; Wolz *et al.*, 2017).

My research at a leaf-scale highlighted the importance of species-specific attributes in driving C fluxes in semi-arid Australia. Integrating plant eco-physiological responses of dominant species is an essential step for improving our understanding of C flux rates within a

Mulga woodland and *Corymbia* savanna. Comparing semi-arid ecosystems contributes to our understanding of ecosystem functioning and mechanisms underlying variability in rates of C and water flux within different ecosystems, which bring us closer to understanding global variability in C cycling in terrestrial ecosystems. The research at a leaf-scale highlighted the importance of species-specific attributes of co-occurring species driving C fluxes in central Australia. Understanding functional processes (i.e., C assimilation, stomatal behaviours plant water status) and the vegetation responses across different plant species and ecosystems is crucial for improving our ability to predict global change. There is now an opportunity to evaluate the inclusion of *in situ* observations and account for variations of C and water fluxes when applying earth systems models and terrestrial vegetation C models at regional- and global-scales.